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THE CONCRESCENCE THEORY OF THE VERTEBRATE EMBRYO.

BY CHARLES-SEDGWICK MINOT.

THIS article, and the one to follow, owe their form to the fact that they have been written as chapters in my *Treatise on Human Embryology*. As this work cannot be published for some time to come, and as the chapters present certain views which are fundamentally different from those currently received by embryologists, I publish them separately. I believe that the right understanding of the early development of vertebrates depends upon the acceptance of Prof. Wilhelm His's view of concrescence. This view has not received the attention it deserves, for it is not based upon elaborate reasoning, but upon the direct observation of the process of concrescence in sundry vertebrates.

Incidentally it will appear that in my opinion neither Hertwig's Cœlomtheorie, nor Rabl's Theorie des Mesoderms, can be maintained for vertebrates; both of these theories involve the assumption that the vertebrate mesoderm arises as two lateral masses. This is true of no vertebrate; on the contrary there is probably hardly another fact in embryology so certainly established by innumerable observations as the fact that the vertebrate mesoderm *arises* as a single axial structure. It is only secondarily by the down-growth of the medullary groove and the up-growth of the notochord, that the mesoderm is divided by the meeting of these structures into two lateral masses. As regards Rabl's theory of the double origin of the vertebrate mesoderm, I think he would not have advanced that theory, had he not first fallen into the error of rejecting Prof. His's concrescence theory.[1]

That the fundamental difference between the mesothelium and mesenchym involved in the Cœlomtheorie cannot be maintained for vertebrates, I have pointed out elsewhere.[2] This impossibility has also been brought out afresh by the investigations of Bonnet, Ziegler, Strahl, Rabl, and others.

As briefly indicated in my article on Segmentation of the Ovum (AMERICAN NATURALIST, 1889, June and September), the vertebrate *diaderm* (stage with ectoderm and entoderm only), advances to the next stage of development by the concrescence of the two halves of the ectental line to form the structural axis of the future embryo. The process is somewhat complex, and needs therefore to be described in detail, the more so as it has still to be traced in mammals.

Historical Note.—The earliest observations on concrescence to form the embryonic axis are, so far as known to me, those of Rathke on leeches.[3] Nine years later, Kowalewski (Mem. Acad. Sci., St. Petersbourg, 7th Ser., XVI., 1871), recorded its occurrence among insects. Its recognition as a vertebrate mode of development we owe to the brilliant investigations of W. His; in his first paper, *26*, he describes very accurately and clearly the process of concrescence in the salmon; in his second paper, *27*, he describes concrescence in the sharks, and in his third paper, *28*, he discusses again the general bearing of his results. Semper in his great work on the relationship of annelids and vertebrates, *54*, was the first to make a direct comparison of the processes of concrescence in annelids, insects, and vertebrates. Unfortunately Balfour entirely failed to grasp the new conception, and by expressing himself very decidedly against it, *Comp. Embryol.*, II., 306–308, led many embryologists to discredit the discovery. Whitman, *67*, 91–94, has ably defended the comparison made by Semper, see above. Rauber, *46*, Kollmann, *33*, Ryder and others, *50*, *51*, have added to our knowledge of the phenomenon. Duval's researches on the chick, *18*, demonstrate concrescence there also, though the author appears unacquainted with the results of his predecessors. Minot, in the article Fœtus, in Buck's Handbook, III., 172, 173, accepts concrescence as the typical mode of vertebrate development.

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[1] Rabl's criticisms of His are very much to be regretted. If the former always observes with the precision and accuracy of the latter, he will add to his already high reputation.

[2] Buck's Reference Handbook, Med. Sci., III., 176.

[3] Rathke and Leuckart, Beiträge zur Entwickelungsgeschichte der Hirudineen, Leipzig, 1862.

Concrescence in Bony Fishes.—At the close of segmentation the germinal disc forms a cap of cells on the yolk. The disc (primitive blastoderm) spreads over the yolk gradually; when it begins to spread its edge is already thickened; this thickened edge corresponds to the ectental line; the thickening is known as the *Randwulst;* it is also called the blastodermic rim, which term Ryder and others have used. When the blastoderm has spread so as to cover perhaps a sixth or less of the surface, one point of the rim ceases to move; consequently as the expansion continues, the edge of the disc bends in behind this point on each side, until two parts of the blastodermic rim meet, as they come from opposite sides, and then grow together. This is illustrated by the accompanying diagram, Fig. 1; *Y* is the outline of the yolk; *bl*, the outline of the blastoderm; *d* the fixed point; the expansion of the blastoderm has brought the parts 1, 1, together, and they have united; the parts 2, 2, are about to meet and unite; then 3, 3, will meet; 4, 4, and so on until the two halves of the ectental line are brought together along their entire length; their junction marks the axis of the future embryo, and produces a longitudinal band of thicker tissue, which has long been known to embryologists under the name of the primitive streak. The primitive streak in the

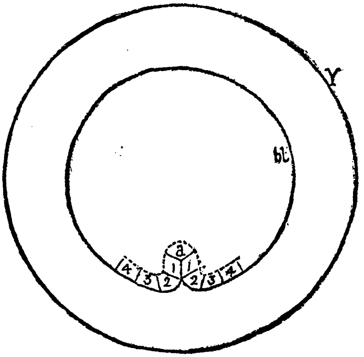

FIG. 1.—Diagram of vertebrate ovum seen from above to illustrate the power of concrescence: *Y*, outline of the yolk; *bl*, blastodermic rim; *a*, fixed point of rim.

anaminota is probably not identical with the so-called primitive streak of the amniota, but rather with the head process as explained later. The fixed point of the blastodermic rim marks the head-end of the embryo; the parts of the ectental line, which grow together next behind the fixed points develop into the head; those a little further back into the neck, and those further back into the rump and tail. The parts of the circular rim most remote from the fixed point, *d*, of course concresce last. The destiny of each portion of the ectental line is fixed before concrescence occurs. In fact in certain cases the differentiation of the tissues advances to a considerable degree in the Randwulst before concrescence. This is strikingly the case in Elacate, in the ova of which the myotomes (or segmental divisions of the mesoderm) appear in the embryonic rim before its concrescence. (Ryder, 1885, *51;* compare also Ryder's observations on Belone, *49*.)

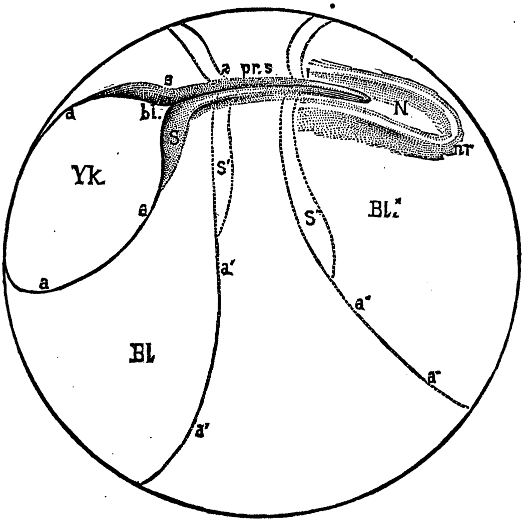

FIG. 2.—Diagram illustrating the growth of the blastoderm, and concrescence of its rim to form the primitive streak, *pr. s*. *N*, neural or medullary groove; *nr*, neural ridges; *Bl*, blastoderm; *S*, part of the blastodermic rim, termed the sichel in German; *pr. s*, primitive streak, *bl*, blastopore; *Yk*, uncovered yolk. Compare also the text.

The accompanying diagram may assist to render clear the process of concrescence, Fig. 2. It is intended to illustrate the spreading of the ectoderm (germinal disc, blastoderm, *auct.*) over the yolk, and the simultaneous formation of the primitive streak. The whole ovum is represented as seen in projection; the proportions are such as have been suggested by the ova of flounders and frogs. Three successive stages of the expanding blastoderm are represented; the first position of the embryonic rim (ectental line) corresponds to the dotted line, *a'' a''*; the concrescence reaches only to the point marked 1; the lateral margins, *s''*, which are to concresce later, still form part of the edge of the blastoderm. At the next stage the ectoderm has grown very much, and has moved its edge to *a'*, *a'*, while the margins, *s*, have coalesced so that the primitive streak extends to 2. The extension continues, bringing the ectental line to *a*, *a*, *a*, *s*, and carrying the primitive streak back to 3; behind the primitive streak a small area, *Yk*, of the yolk is still uncovered, and corresponds to the so-called anus of Rusconi in frogs' ova. The portion of the ectental line bounding this area differs from that which is immediately concerned in the formation of the primitive streak, *s*; although it now lies behind the primitive streak, it was previously in front of it, when the blastoderm covered only the minor portion of the ovum. (See *s''*, *a'' a''*.) Ultimately the yolk is entirely covered by the blastoderm, thus fixing the length of the primitive. streak. It is essential to notice that the blastodermic rim (ectental line) divides into two portions, one, *s*, which forms the primitive streak, and another, *a''*, *a''*, which overgrows the ovum and at last closes over the yolk behind the completed primitive streak. That the processes are essentially as described becomes evident upon examination of the figures given by W. His, *26*, Kupffer, *39*, Coste, *14*, and others.

Underneath the entire length of the band of cells constituting the primitive streak is formed a cavity, which is transformed ultimately into the cavity of the alimentary canal and its appendages. It is termed the archenteron or entodermic canal (*Urdarm*). The mode of concrescence in elasmobranchs elucidates the formation of this cavity. In bony fishes the cells which form the walls of the archenteron lie so close together that the lumen of the canal is obliterated and does not appear until considerably later (*cf.* Balfour, Comp. Embryol., II., 75.)

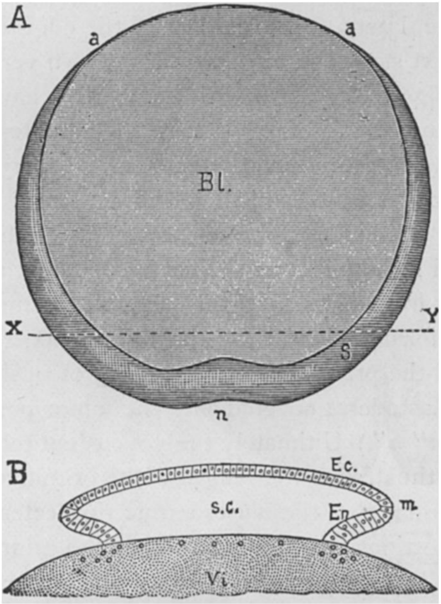

FIG. 3.—Diagram of an elasmo branch blastoderm to illustrate the formation of the marginal groove. *A*, surface view; *Bl*, blastoderm; *a*, *a*, anterior grooveless margin; *S*, (*Sichel*) marginal groove; *n*, marginal notch; *X*, *Y*, line of sections; *B*, section along the line *X*, *Y*, of *A*; *Ec*, ectoderm; *En*, entoderm; *m*, ectental line; *s. c.*, segmentation cavity; *Vi*, yolk with nuclei.

Concrescence in Elasmobranchs—Our knowledge rests mainly on the researches of His., 27, and his follower Kollmann, 33. Fig. 3, *A*, is a generalized diagram of an elasmobranch ovum, representing the ectodermal disc, *Bl*, as seen from above, resting upon the yolk, which is not represented in the figure. The first change noticeable in the disc after the close of segmentation is a groove running completely around its margin, between it and the yolk; as the disc grows and expands, the groove is no longer present along the front edge, *a*, *a*, of the blastoderm, but only on the sides and behind. About the same time there usually appears a distinct notch, *n*, which marks the fixed point of the margin, and the posterior end of the disc. If, now, a section be made across the line, *x*,*y*, the relations will be found to be essentially as represented in the diagram, Fig. 3, *B*; the disc rests on the yolk, *Vi*, which contains numerous nuclei; between the yolk and the ectoderm, *Ec*, is the segmentation cavity, *s. c.*; the groove is bounded above by a layer of cells, *en*, which are larger than those of the ectoderm, and have been produced by the yolk, *Vi*; sometimes there are cells lying in the segmentation cavity at this stage, the formation of the mesoderm having already begun. The essential point to note in this stage is, as Kollmann has shown, the division of the margin of the ectodermal disc into two parts, one, *a*, *a*, resting directly on the yolk, the other *s*, directly continuous with a layer of entodermal cells, *B*, *En*, forming a little groove under the margin of the disc. The two portions of the ectental margin have entirely distinct functions, as already stated: the interior, *a*, *a*, is destined to grow over and cover the yolk by the extra-embryonic portion of the ectoderm: the posterior, *S*, is destined to form the primitive streak of the embryo.

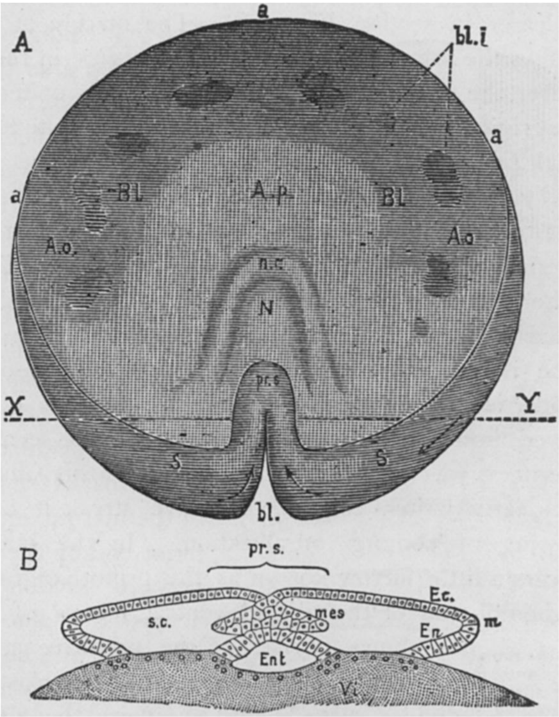

FIG. 4.—Diagram of a vertebrate blastoderm a little more advanced than Fig. 3.—*A*, surface view; *B*, section along the line *X*, *Y*; *Bl*, blastoderm; *a*, *a*, *a*, anterior margin *s.s.*, posterior margin (Sichel); *A*, *o.*, area opaca; *A.p*, area pellucida; *n.r.*, neural ridges; *N*, neural or medullary groove; *pr.s.*, primitive streak; *bl*, blastopore; *Ec.*, ectoderm; *m*, ectental margin; *En.*, entodermic cells; *Vi*, yolk; *mes.*, mesoderm; *s.c.*, segmentation cavity.

Fig..4 is similar to Fig. 3, but represents a more advanced stage. The ectodermal disk, *Bl*, is much enlarged, and its anterior grooveless margin, *a*, *a*, *a*, is relatively much more increased than the posterior grooved margin *S*; the centre of the notch, Fig. 3, *n* has remained nearly if not quite stationary, Fig. 4, *pr.s.*, while the margin, *s. s.*, of either side has been growing toward its fellow in the manner indicated by the arrows, and as they meet the two side margins grow together in the median line, making a longitudinal structure. The manner and results of the concrescence of the margins from the two sides to form a median longitudinal structure, become clearer in section, Fig. 4, *B*. The margin at the side, *m*, still shows the same relations as in Fig. 3, *B*; in the median line, however, the margins have met and intimately united, so that what were originally two grooves have completely united to form a single canal, *Ent*, bounded above by entodermal cells, below by the entodermal yolk, *Vi*. This canal is the primitive entodermal cavity. A moment's consideration renders it evident that the canal must be open posteriorly; this opening is the blastopore, *bl*. There are some further details to be mentioned; where the ectental margins have united in the median line, there appears a lateral outgrowth, *mes*, which is the beginning of the mesoderm; in some cases this mesodermic tissue appears before the margins concresce; when viewed from the surface the mesoderm can be seen through the ectoderm, as was observed long ago; it is this faint appearance which early writers call the primitive streak, it being the foreshadowing of coming organization. In the middle line there appears a little furrow known as the primitive groove, perhaps the homologue of the ciliated ventral furrow of annelids. The Fig. 4, *A*, also shows *in front of* the primitive streak the first trace, *N.*, of the central nervous system. The blastoderm is seen also to be divided already into two parts, the lighter area pellucida, *A. p.*, and the darker area opaca, *A. o.*; the latter also shows the first blood islands.

From their observations, His, Kollmann and others have inferred that at the anterior ectental margin, *a*, *a*, *a*, there are produced (from the yolk) cells, which grow in toward the embryo, and constitute part of the mesoderm, and are especially concerned in forming the first blood, which is produced always in the extra-embryonic area. This mesoderm of peripheral origin His has named parablast, a term which unfortunately has been employed differently by some subsequent writers. The ectoderm, entoderm, and axial mesoderm Prof. His groups under the collective name of archiblast. This view of the double origin of the mesoderm, although it has been adopted in a modified form by the brothers Hertwig, I am unable to accept.

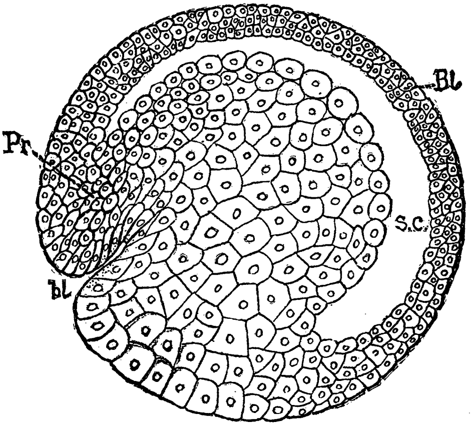

FIG. 5.—Ovum of axolotl; after Bellonci; longitudinal section to show the commencing formation of the primitive streak; *bl*, blastopore; *Bl*, blastoderm; *s.c.*, segmentation cavity.

Concrescence in Marsipobranchs, Ganoids and Amphibians. — As not only the constitution of the ovum, but also its early development, is very similar in the three classes named, we may consider them collectively in the present connection. The condition of the ovum at the close of segmentation I have already described,[3] p. 472 and figured, Fig. 4, *3*. The ectental line is not sharply defined, nor does there appear any groove around the edge of the blastoderm as in meroblastic ova. The small-celled ectoderm spreads over the yolk; while it is doing this a small cavity appears at the hind edge of the blastoderm, with a small opening to the exterior known as the blastopore, Fig. 5, *bl.;* the cavity runs forwards towards the segmentation cavity Fig. 5, *sc.;* above and in front of the blastopore the cells have multiplied and accumulated to form the beginning

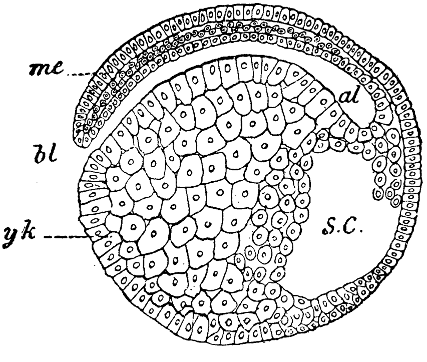

FIG. 6.—Ovum of Petnmyzon in longitudinal section, after Balfour.

[3] AMERICAN NATURALIST, 1889.

of the primitive streak, *Pr.* In the lamprey there is at this stage no such accumulation of cells; according to Shipley the ectoderm consists of a single layer of cells and the archenteron is bounded on its dorsal side by a single layer of cells also, between which and the overlying blastoderm there are no cells; the gathering of cells, corresponding to the primitive streak, does not arise until later. The cavity becomes that of the anterior end of the archenteron; it is sometimes designated as the blastoporic invagination. The archenteron, in the same measure as the blastoderm spreads over the yolk, grows at its hinder end away from the segmentation cavity, Fig 6, just as in elasmobranchs. A stage is soon reached in which nearly the entire length of the archenteron is formed, and nearly the whole yolk is covered. There is still a blastopore which leads into the cavity, and which has moved gradually backwards from its original position. Behind the blastopore lies the uncovered yolk, which in the frog's ovum is very conspicuous, because its whitish color contrasts with the dark color of the heavily pigmented ectoderm around it; this area of exposed yolk is the so-called anus of Rusconi. When the archenteron has completed its full length, the following disposition of the parts is found, Fig. 7. The archenteron is bounded below by the large mass of yolk cells, *vi,* and above by the epithelium, *ent,* of the entoderm; its posterior end curves up to open at the blastopore, *Bl,* passing through a mass of cells, which constitutes the hind end of the primitive streak; this portion of the archenteron is sometimes called the blastoporic canal. There is further a short prolongation, *Al,* of

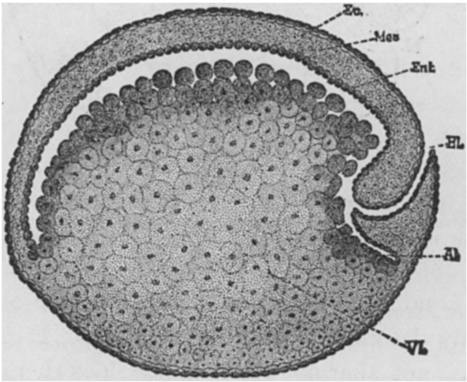

FIG. 7.—Longitudinal section of the ovum of a sturgeon after the formation of the entodermic cavity. *Ec,* ectoderm; *mes,* mesoderm; *Ent,* entoderm; *Bl,* blastopore; *Al,* diverticulum of the archenteron; *Vi,* yolk (after Salensky).

the cavity below the blastopore. This diverticulum has been homologized with the allantois. It is also very probably homologous with the more nearly spherical diverticulum found in a similar position in teleosts, and now known as Kuppfer's vesicle, from having been especially studied by C. Kuppfer, *34*, *35*, who has interpreted it as the teleostean allantois. Compare D. Schwarz, *53*, 197, Taf. XIII., Figs. 35, 37, etc. Around the blastopore is a mass of cells, continuous on the one side with the ectoderm, on the other with the epithelial entoderm lining the archenteron, and thirdly with a sheet of cells, *mes*, between the ectoderm, *ec*, and entoderm, *ent*.

The developmental phases just outlined seem to me to afford sufficient evidence of concrescence. Owing to the gradual transition between the ectoderm (blastoderm) and the entoderm (yolk cells), there is no sharp ectental line as in some types. Moreover there is no differentiation of the tissues at the blastodermic rim, but only after the cells are united in the axis, hence we cannot distinguish parts at the periphery of the blastoderm and follow their union in the primitive streak as we can in certain sharks and bony fishes. Nevertheless we find all the essential features of concrescence; the entodermal canal and the primitive streak begin at the edge of the blastoderm and grow at their posterior end away from the segmentation cavity and at the same rate the blastoderm overspreads the yolk.

Concrescence in Sauropsida.—The early development of the reptilian ovum is imperfectly understood, although several valuable memoirs have been published upon it. The ova present the peculiarity that the posterior end of the primitive streak is a solid mass, the blastoporic canal being closed until a quite advanced period, when it is temporarily opened. (Compare the section on the *Blastopore.*) It seems to me that the archenteron is formed by concrescence, in spite of the modified history of the blastoporic canal. Not only does the primitive streak begin its development at the edge of the primitive ectoderm (blastoderm or germinal disc) and grow backwards, but also the ectodermal cavity is formed underneath it, but there is no open blastopore so far as yet observed. This growth of the primitive streak and groove are very clearly demonstrated in C. Kuppfer's figures, *36*, Taf. VIII., Figs. 1-3. Moreover, Kuppfer and Benecke have found, in certain cases, the so-called "Sichel," or transverse thickening at the hind end of the growing primitive streak; this thickening is a portion of the blastodermic rim, and by the interpretation I adopt until better observations shall decide, it corresponds to the transverse thickening in a similar position in sharks.

The process of concrescence in birds was partly indicated by Koller's investigations, *30*, *31*, and has been carefully elucidated by Duval, *18*, I. The resemblance to concrescence as known in elasmobranches is very striking. Around the edge of the blastoderm appears very early a small groove; as the blastoderm expands the front portion loses the groove; one point, the centre of the groove, ceases to move, or at least moves much more slowly than the remainder of the blastodermic rim; as the expansion continues the edges of the two halves of the groove coalesce gradually behind the fixed point, thus producing the entodermal canal in the same manner as in sharks; cells accumulate at the same time and make the so-called primitive streak; most of these cells enter into the composition of the mesoderm. There is an uncertainty in Duval's account owing to his failure to distinguish between the segmentation and the entodermal cavities; as I have pointed out, AMERICAN NATURALIST, 1889, p. 475, Duval's subgerminal-cavity at the close of segmentation is the true segmentation cavity (blastocœle); his own account of the concrescence shows that the entodermal canal arises separately and behind the blastodermic or true segmentation cavity; but unfortunately neither his text nor his figures give satisfactory information in regard to the separation of the two cavities; Duval calls the entodermal cavity also the subgerminal, thus causing confusion, since subgerminal is properly applied only to the blastocœle.

In birds (hen's ova) there is a further peculiarity, which is, I think, probably to be found in all amniota, namely:—that portion of the edge of the ectoderm which does not share in concrescence, and which corresponds to the edge of the anus of Rusconi, closes over the yolk behind the primitive streak, so that the portion of the yolk which is left uncovered is remote from the embryonic area (or primitive streak). As a rare anomaly (see Whitman, *68*), a line is visible running in the ectoderm from the hind end of the primitive streak to the edge of the uncovered yolk; this line is to be interpreted as evidence of the growing together of the ectoderm behind the streak proper. The ectoderm, as it spreads over the yolk, receives no accretions from it, but accomplishes its expansion by proliferation of its own cells. Thus the uncovered yolk is bounded by the free edge of the ectoderm; this area, which may be called the yolk blastopore,[5] is comparable to the anus of Rusconi, from which it differs in position, being remote from, instead of close (as in the anus of Rusconi) to the primitive streak, for it is situated nearly opposite the embryonic area. In birds, according to Duval, *19*, the yolk blastopore (Dotternabel) is never closed by ectoderm, but remains covered by the vitelline membrane only until the mesoderm spreads over it. The growing edge of the ectoderm is somewhat thickened; it finally is reflected around the edge of the yolk blastopore, forming as it were a funnel, at the bottom of which is the yolk. (See Duval, *l. c.*)

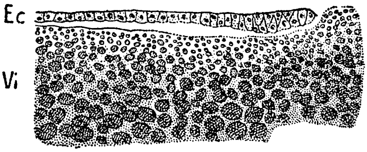

FIG. 8.—Hen's ovum; incubated six hours; anterior edge of the ectoderm, *Ec*, resting on the yolk, *Vi*; from a longitudinal section of the blastoderm in situ; after Duval.

Concrescence in Mammals.—There is, as yet, no direct evidence of concrescence in mammals, but strong indirect evidence. First, it is to be remarked that of no mammal do we know the exact history of the primitive streak, and secondly that what we do know accords fully with the history in the Sauropsida. There is a primitive blastoderm on the edge of which the primitive streak appears, and from its beginning the streak grows backwards as the germinative area expands. Now the mammals are derived from the reptiles, and it may be assumed safely that their early development is essentially the same as that of the reptiles, and what knowledge we possess agrees with this inference. Unfortunately the few authors who have investigated the primitive streak in mammals have failed to consider the problem, as the discoveries of His and his followers have rendered it necessary to consider it, namely, as the question: How is concrescence modified in mammals? It is therefore not surprising that we lack the necessary information. The organization of the mammalian primitive streak is described below. Provisionally, at least, we must assume that the streak follows the same developmental type in the highest as in the lower vertebrates.

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[5] Duval applies to it the name of ombilic ombilical.

Concrescence, Summary.—The evidence that concrescence is the typical means of forming the primitive streak in vertebrates is: (1) detailed and conclusive observations upon elasmobranchs, teleosts and birds; (2) exact and extensive observations on marsipobranchs, ganoids and amphibians, which concord with the theory of concrescence; (3) a great probability of its occurrence in reptiles, owing to the similarity of their development with that of birds; (4) a probability of its occurrence in mammals, because of the resemblance in the growth and structure of the primitive streak to that in other vertebrates. It seems to me therefore not premature to draw the generalization that *the vertebrate primitive streak is formed by the growing together in the axial line of the future embryo of the two halves of the ectental line.*

The development of the primitive streak may be described in general terms as follows:—At the close of segmentation the edge of the primitive blastoderm separates into two parts; one part (the anterior), as the blastoderm expands, spreads over the yolk, gradually covering it with ectoderm; the other part (the posterior) forms the primitive streak; it has in its centre one fixed point, consequently when the blastoderm expands the two halves of the posterior part of the ectental line are brought together, and gradually unite (concresce) along a line running from the fixed point radially backwards as regards the blastoderm. Consequently the segmentation cavity which is underneath the primitive blastoderm lies in front of the developing archenteron. While this goes on, cells grow out from the concrescing part of the ectental line into the space between the ectoderm and entoderm (or yolk); underneath the line of junction a cavity is formed, lined by entoderm, having cells on the dorsal, yolk on the ventral side; this cavity with its walls is the archenteron; the archenteron lengthens backwards as concrescence progresses; it has, whatever its length, a small entrance (the blastopore) at its hind end; the blastopore is ultimately obliterated; it is found to be temporarily closed in (all?) amniota during the lengthening of the archenteron (and primitive streak). The cells which grow out from the ectental line constitute the first anlage of the middle germinal layer or mesoderm, and shining through the ectoderm they produce the appearance of a whitish line, which has led to the name of primitive streak. The characteristics of the mesoderm are described in the next section. Along the line of junction there often appears a slight furrow in the ectoderm, which is known as the primitive groove.

Significance of Concrescence. It will at once be evident that if the process of concrescence went on without the actual meeting of the two portions of the ectental line the result would be to leave the archenteron open along its entire length; the borders of the opening would be the ectental line; and this line, as I have shown elsewhere (AMERICAN NATURALIST, 1889), corresponds to the lips of the gastrula mouth; consequently we should have a gastrula with an elongated mouth. This condition is illustrated by the accompanying diagram. It agrees in all respects with the gastrula type; its most noteworthy peculiarities are two:—*first*, the enormous mass of yolk accumulated in the aboral portion of the entoderm; *second*, the elongation of the gastrula or archenteric cavity in a direction at right angles to the gastrula axis, *Xy*. If now the lips of the gastrula, Fig. 9, meet, and unite we should obtain at once the vertebrate type, cf. Fig. 4, B. Accord-

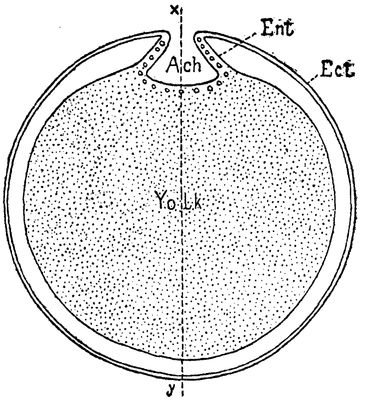

FIG. 9.—Diagram of a vertebrate embryo in which the lips of the gastrula mouth are supposed not to have concresced. *Ach*, archenteron; *Ent*, entoderm; *Ect*, ectoderm; *Yolk*, yolk-entoderm; *x-y*, gastrula axis.

ing to His's discovery this is precisely what takes place, only the lips are brought together first at one end, where they at once unite, while behind they are widely separated; but gradually they are brought together and unite throughout their entire length.

Concrescence is, then, a modified method of uniting the lips of a greatly elongated gastrula mouth. Why this modification is established we cannot say with certainty, though we may surmise with confidence that it is consequent upon the great accumulation of yolk in vertebrate ova.

The view here adopted enables us to speak positively as to the point where we are to look in vertebrates for the homologue of the invertebrate mouth. In annelids concrescence is very well marked whenever the ova contain much yolk; now in leeches and earthworms, the ectental line does not concresce along the entire axial line but on the contrary, as shown by Kleinenberg and Whitman, the foremost part of the germ bands (gastrula lips) do not unite but leave a small opening; when the permanent mouth is formed this opening is carried in and serves as the passage between the mouth cavity (Vorderdarm, stomodæum) and the archenteric cavity. The foremost part of the line of concrescence lies according to His' observations on fishes just where the optic outgrowths arise; hence we have to search between the origins of the optic nerves for traces of the invertebrate mouth.

(*To be continued.*)